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Diminishing return of investment in genetic diversity

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ABSTRACT

Motive: Priorities in conservation management are often difficult to determine because we lack comparable biodiversity metrics. So that actions can be cost-effective, conservation decision-making and management needs such metrics.

Question: What suitable metrics can compare efforts and investments in biodiversity conservation? How can established measures of genetic diversity be combined with the economic return-of-investment paradigm?

Method: Use the return-of-investment approach, which has previously been restricted to issues of species diversity. Extend it to include genetic diversity. Use Taylor's power law to relate mean abundance, rates of genetic deterioration, and principles of return-of-investment.

Key assumptions: We can specify the relationship between cost of conservation and population size. Time-series data are available for each population. We can approximate the effective population size (N_e) of a fluctuating population as the harmonic mean population size.

Conclusion: As the financial investment in conservation increases, the estimated marginal increase in genetic diversity diminishes. One can rank actions that increase mean population size according to their associated marginal increases in genetic diversity, thus evaluating which improvements offer the most value for money.

Keywords: adaptive potential, biodiversity, conservation, diminishing returns, genetic diversity, return of investment.

INTRODUCTION

Owing to the wide discrepancy between the means required to safeguard biodiversity and the resources nations and communities are willing to devote to conservation, ways are needed to allocate those resources (Weitzman, 1992; Wilson *et al.*, 2006). To this end, a number of

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studies have recently applied the return-of-investment (ROI) approach to conservation resource allocation problems. Recommendations have been made to make any assessments as precise as possible, such as taking account of the precise costs of the conservation efforts (Naidoo *et al.*, 2006; Murdoch *et al.*, 2007; Bode *et al.*, 2008; Carwardine *et al.*, 2008) and the spatial heterogeneity of socioeconomic factors (Chan and Daily, 2008; Polasky *et al.*, 2008). The ROI approach has been shown to be more effective than other methods in improving the efficiency of conservation investment and in ensuring better biodiversity preservation when resources are limited (Ando *et al.*, 1998; Murdoch *et al.*, 2007; Carwardine *et al.*, 2008). Usually, such analyses aim to maximize the number of species or number of endemic species protected, which in turn is based on the species–area relationship (MacArthur and Wilson, 1967). Previously, ROI has focused on (i) conservation from a demographic perspective and (ii) conservation of habitat types. An important yet neglected aspect of conservation is the maintenance of genetic diversity and viability (Schwartz *et al.*, 2007). Here, we expand the approach to accommodate this aspect because the sustainability of species and habitats ultimately depends on genetic viability. Obviously, many natural populations of the same species are interconnected and hence mutually influenced demographically and genetically by adaptive migration and range expansions (Bach *et al.*, 2007; Travis *et al.*, 2010).

By applying the principles of ROI to conservation genetics, we hope to distinguish among population conditions and conservation options to identify those which provide the highest marginal genetic diversity return per unit investment. In other words, we suggest equating ROIs across conservation options, not to maximize ROI *per se*, but to maximize genetic diversity.

To apply the principles of ROI to the conservation of genetic diversity, we use Taylor's law, which relates a population's mean abundance to variability in abundance, and the harmonic mean, which relates variability in abundance to the rate of genetic drift. These relationships represent a useful basis for assessing ROI because of their application to a wide range of taxa and, more generally, because much is known about how populations fluctuate (Pimm, 1992; Arino and Pimm, 1995). Because they are based on such general relationships, the results from our ROI analysis are also of general value. Moreover, the principles on which our analysis is based could be applied to specific cases for which information is available on the abundance–variability relationship.

Although the demographic properties of a population may make it appear viable, long-term viability can be severely compromised by the loss of genetic diversity (Keller and Waller, 2002; Spielman *et al.*, 2004). For this reason, the conservation of biodiversity requires enough genetic diversity to ensure the evolutionary potential necessary for populations living in changing environments. Two aspects of such genetic diversity are the rate of inbreeding and relative strength of genetic drift, which are each directly related to a population's effective population size (N_e). The amount of genetic variability present in a population is closely related to N_e (Frankham, 1996). The notion of N_e is therefore central to the relationship between ecology and genetics and such ecological characteristics as demography, life history, and social structure, while N_e in turn determines the speed at which the population loses genetic variability (Goldstein and Pollock, 1997; Vucetich and Waite, 1999). Furthermore, in fluctuating populations N_e is closely (inversely) related to the risk of extinction, since the temporal harmonic mean population size (HM) is the surrogate measure for N_e and HM is mainly determined by the minimum population sizes in a certain time interval. Very large fluctuations are typically observed in small mammals and heterotherms, but when fluctuations are measured on a per-generation basis they can be of the same magnitude in

large mammals (Sibly *et al.*, 2007). Since in the main N_e is determined by the minimum point, and the closer the minimum point is to zero the higher the extinction risk, we argue that N_e helps to predict extinction risk (Vucetich and Waite, 1999; Pertoldi *et al.*, 2008). Given that the increase in inbreeding level (F) is related to N_e, we can deduce that the minimum point also determines the rate of increase in F per generation.

The advantage of our assessment of the marginal gain in biodiversity is that it is based on established theory and allows comparative analyses potentially applicable both to single species and to communities. The requirements are basically a number of time series for populations at different mean population size and the cost of maintaining the population at a certain size (typically closely related to the price of land). To our knowledge, no previous study has used the ROI conservation approach in the context of genetic diversity of candidate populations. Our goal here is to introduce the conceptual framework; elsewhere we will deal with its application to case study populations.

RESULTS

In evolutionary ecology, the magnitude of population fluctuations scales systematically with mean abundance (e.g. Desharnais *et al.*, 2006). For example, for a population experiencing constant per capita environmental variability, the regression of $\log \sigma^2$ (variance) versus $\log \overline{\mu}$ (arithmetic mean) gives a line with a slope of 2 and this positive relationship between σ^2 and $\overline{\mu}$ can be described using Taylor's power law (Taylor, 1961),

$$\sigma^2 = K\overline{\mu}^{\beta}, \tag{1}$$

where K is a constant and β a scaling coefficient. Larger values of β indicate that the variance increases more rapidly with $\overline{\mu}$ than expected. Values of $\beta > 2$ are not exceptional, and it has been suggested that β may lie anywhere in the range of 0.6 to 2.8 for animal populations (Taylor and Woiwod, 1982). Taylor and Woiwod (1982) estimated β for 97 aphid species; for 31 of these species, β was found to be above 2. Cases of β with values well above 2 were also demonstrated in the models presented by Keeling (2000). Furthermore, Pertoldi *et al.* (2007) suggested that increasing environmental variability raises the value of β, so that in populations where β is initially below 2, an increase in environmental variability can take β above the threshold value of 2.

Using equation (1), Pertoldi *et al.* (2007) demonstrated that the harmonic mean of a population's size is approximated by (Fig. 1)

$$HM = \overline{\mu} - K\overline{\mu}^{(\beta-1)}. \tag{2}$$

Because HM also estimates N_e (Wright, 1931), one can use equation (2) to quantify how N_e increases with $\overline{\mu}$.

In addition to loss of variability by random genetic drift, inbreeding (defined by the probability, F, of two randomly chosen alleles being identical by descent) also reduces genetic diversity in small populations. Specifically, F increases each generation according to $\Delta F = 1/2\ N_e$, hence by substituting N_e with (2) we can express the change in the rate of inbreeding as

$$\Delta F = \frac{1}{2(\overline{\mu} - K\overline{\mu}^{(\beta-1)})}. \tag{3}$$

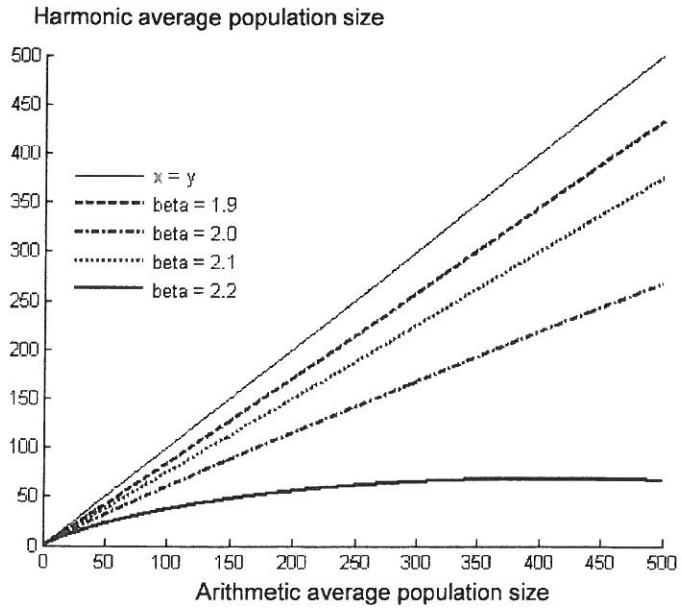

Fig. 1. Numerical examples of equation (2) showing how the harmonic average relates to the arithmetic average for various values of β (with $K = 0.25$).

Figure 2 illustrates how the rate of inbreeding decreases as a function of the arithmetic mean population size.

As noted by Pertoldi *et al.* (2007), the first derivative of equation (2) with respect to $\overline{\mu}$,

$$\frac{\partial \mathrm{HM}}{\partial \overline{\mu}} = 1 - K(\beta - 1)\overline{\mu}^{(\beta-2)}, \tag{4}$$

describes where the trajectory of the HM as a function of $\overline{\mu}$ inflects from positive to negative. In the context of ROI, this means that we can identify putative domains of negative returns of investment in increasing the mean population size. As shown in Figs. 3a and 3b, the ROI can follow qualitatively different scenarios of return patterns. Such knowledge is important for managers when choosing which populations conservation efforts should be directed at.

Our objective is to characterize how benefits, in the form of enriched genetic diversity, result from investment in larger average population sizes. It is useful to focus on the largest possible marginal return. Let Δg define the (positive) change in genetic diversity resulting from the combination of forces acting at a given arithmetic mean population size. We can then express the goal of maximizing the marginal gain as

$$\max(\Delta g_{i,j}/\Delta \cos t_{i,j}) \tag{5}$$

where $\Delta g_{i,j}$ is the change in genetic diversity of species i in population j and $\Delta \cos t_{i,j}$ is the corresponding conservation investment.

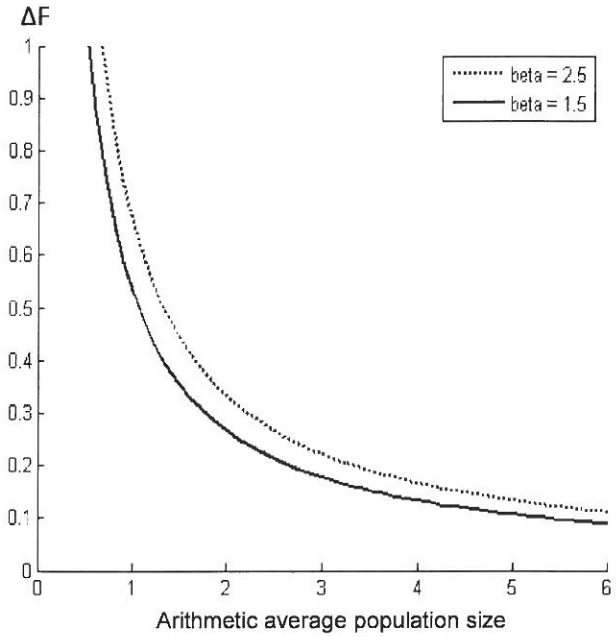

Fig. 2. ΔF as a function of arithmetic average population size with $K = 0.25$ and $\beta = 1.5$ or 2.5.

If we suppose that the cost of a protected area is linearly related to the mean population size, we have

$$\max(\Delta g/\Delta \cos t) = \max(\partial \mathrm{HM}/\partial \overline{\mu}) = \max(1 - K(\beta - 1)\overline{\mu}^{(\beta-2)}). \quad (6)$$

For non-negative values of $\overline{\mu}$, and for all values of K and $\beta < 1$, the maximum value for the rightmost expression in equation (6) is $\overline{\mu} = 0$. This means that when maximizing the ratio of gain to cost based on equation (5), the population is zero and no land has been conserved. Clearly, this demonstrates that the marginal gain *per se* should not be the focus of the analysis, but rather used for the purpose of comparison. These properties of equation (6) are not unique to applications of ROI to genetic aspects of conservation. They apply to any circumstances in which the benefit to conservation (in this case, g) increases as a decelerating function of *cost*.

DISCUSSION

Preservation of species diversity is important and the irreversibility of losing species remains a challenge. For a given species, priorities may have to be set between different populations from different locations and here our proposed approach could play a role in ensuring the greatest estimated gain in genetic diversity.

There are, however, several other complications associated with the preservation of biodiversity and/or genetic variability. A long-standing debate in ecology is concerned with the effect of diversity on the temporal stability of biological systems. The ecological consequences of biodiversity loss have received increasing attention over the past decade

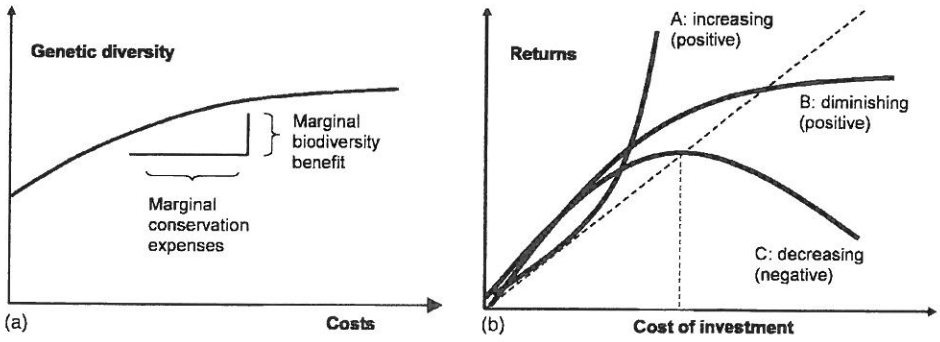

Fig. 3. (a) Marginal genetic diversity return of investment, where the cost is related to the price of land area assumed to map directly onto the number of individuals. Cost can be defined as (number of individuals/area) times the cost of area, thus including heterogeneity in the quality/cost ratio. (b) The qualitative differences among the returns scenarios. Note that the vertical dashed line corresponds to equation (4) being zero.

(Bangert *et al.*, 2005; Reusch *et al.*, 2005). Current theory suggests that diversity has contrasting effects on the temporal stability of populations and communities (Tilman, 1996). Theoretical work suggests a paradoxical effect of diversity on the temporal stability of ecological systems: increasing diversity should result in decreased stability of populations, whereas community stability is enhanced (Tilman, 1996). While empirical work corroborates that community stability tends to increase with diversity, investigations of the effect of diversity on populations have not revealed any clear patterns. This consideration, together with the observation that changes in vital rate may have opposing effects on growth rate and N_e, is important as it can produce disagreement about optimal management strategies. It is well known that demographic instability in a population is translated into fluctuations of N and a reduced N_e that is close to the harmonic mean of the varying N values (Vucetich *et al.*, 1997). Therefore, a management strategy with the goal of preserving biodiversity at the community level could theoretically lead to a reduction of N_e in single populations. In the same way, the attempt to increase growth rate in a population by modifying some of the vital rates can also result in a reduction of N_e. An increase in growth rate will increase N and therefore reduce the demographic stochasticity that is related to the population risk of extinction, but may simultaneously lead to a reduction of the genetic diversity due to stronger fluctuations.

An additional complication derives from the fact that the advantage of having genetic variability stems from considering short- and long-term adaptability and evolution in a changing environment. However, this is not universally true; for example, in a constant environment genetic variability in a quantitative character creates a segregational load each generation due to stabilizing selection against individuals that deviate from the optimum phenotype (Lande and Shannon, 1996). Consider a presumably common situation where natural selection acting on quantitative characters favours intermediate phenotypes. In an intermediate-optimum model, the genetic variability may be either beneficial or detrimental, depending on the pattern of environmental change (the frequency, the amplitude, and the degree of autocorrelation of the environmental oscillations) (Lande and Shannon, 1996; Ranta *et al.*, 2008; Björklund *et al.*, 2009, 2011).

In spite of complicating issues, we believe that this method in combination with other economic metrics of preservation efforts can provide a useful approach to managers and decision-makers for comparisons between populations and the subsequent setting of priorities on an informed basis. In addition, the above demonstration of problems by focusing exclusively on maximizing marginal gain is valuable because one goal for the field of ecological economics is to understand which principles of conventional economics will need to be revised and which are appropriate for societies committed to conservation.

Another benefit of this description of population dynamics and genetic diversity is that potentially it would be possible to suggest whether two (semi)-separate populations or one single larger population provides the most conservation value for money. This kind of question has been referred to as the SLOSS debate (see Higgs and Usher, 1980; Simberloff, 1988). Given the diminishing returns relation observed above, we can conclude that expenditures give the highest 'genetic' payoff when distributed among several small populations, *ceteris paribus*. Although our proposed analysis only requires population size data, the use of ROI to guide the conservation of genetic diversity could be developed towards more specific analyses. If available, it may be constructive to include detailed genetic information of the populations in question such as, for example, the genetic diversity associated with QTL markers for ecologically relevant traits. It should be stressed, however, that molecular markers may be very species specific and even population specific, which means that variation in the abundance–variability relationship may bias analyses in terms of comparisons.

Expecting to find the perfect unambiguous prioritization tool is bound to fail; however, we wish to stress the point that from population data sets we can obtain an indication of the actual gain (loss) of expanding (lowering) the mean population size. This will allow a comparison of conservation scenarios in order to determine the best return of investment providing (biodiversity) value for (conservation) money. To our knowledge, no attempt has been made to implement the concept of N_e and genetic diversity measures in the ROI conservation tools developed to date.

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